7-29-2016

Coral Persistence to Ocean Warming via Developmental Acclimation

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"Coral Persistence to Ocean Warming via Developmental Acclimation"

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Submitted to the Faculty of
Nova Southeastern University
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in

Marine Biology

Nova Southeastern University

July 2016

Thesis of
HEATHER SCHANEEN

Submitted in Partial Fulfillment of the Requirements for the Degree of

Masters of Science:
Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

July 2016

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ABSTRACT:

Scleractinian corals are the 'engineers' of tropical coral reef ecosystems. Their three-dimensional structure provides habitat for thousands of fish and invertebrate species. The persistence of corals is threatened by climate change. In this study I investigated if corals may be able to increase tolerance to ocean warming through developmental acclimation, i.e. if corals that experience warmer temperatures during embryonic and larval development are better able to cope with higher temperatures later in life. Larvae of the broadcast spawning coral *Montastraea cavernosa* were raised at ambient (29°C) and future projected ocean warming temperatures (+2°C, 31°C). After larval settlement, coral juveniles from each treatment were split and reared for two months at either current or +2°C conditions. Larvae reared at the warmer temperature had lower survival and displayed a smaller size at settlement. Juveniles that were in the warmer conditions had faster growth rates. Individuals raised during larval and juvenile stages at 31°C had faster growth rates than individuals only in the elevated temperature treatment after settlement, thus indicating that developmental acclimation may have occurred. However, the highest mortality also occurred in this treatment, therefore the growth results could also be explained by positive selection of the most thermally tolerant individuals. My results suggest that acclimation and/or directed selection may help corals withstand future rises in ocean temperature.

KEYWORDS:

Montastraea cavernosa; developmental acclimation; coral larvae; ocean warming; climate change; latent effects

1. INTRODUCTION

1.1 The importance of corals and existing threats to their persistence

Tropical coral reefs are among the most complex and diverse marine ecosystems (Jackson et al. 2001). The framework of coral reef ecosystems is made up of scleractinian (stony) corals that provide a three-dimensional habitat for thousands of fish and invertebrate species (Jones et al. 1994, Roberts et al. 2016). This framework of calcification and reef accretion aids in increasing biodiversity by providing a variety of hard and stable substrates to support a complex ecosystem (Hughes et al. 2003, Wild et al. 2011). Reefs offer an assortment of ecological services and are of economic value to humans. Ecosystem services that coral reefs provide are vital to coastal communities through shoreline stabilization and act as a buffer to strong storms (Moberg & Folke 1999, Perry et al. 2011). More than one-third of the human population lives near coastal areas where population density is often three times higher than inland (Barbier et al. 2008). Reefs also provide physical protection in tropical areas that aid coastal communities in supporting their currently developed state (2010 US Census, Hughes et al. 2014). Land lost to erosion can prove to be costly; it is estimated that between US $820-$1,000,000 per km was lost due to decreased coastal production (Cesar 1996). In addition to physical services, reefs play a vital economic role in several industries such as fishing, tourism, construction, and medicine (Hoegh-Guldberg 1999). It is estimated that goods derived from coral reefs total $375 billion each year (Veron et al. 2009).

While coral reef ecosystems provide a substantial amount of services and economic value to humans, they are considerably damaged by direct and indirect anthropogenic impacts. Direct impacts include activities such as overfishing, excess nutrient inputs, pollution, reef mining, and dredging (Liu et al. 2009, Kroon et al. 2014). Indirect impacts include herbivorous fish loss and removal of large predators resulting in phase-shifts from a coral-dominated to algal-dominated ecosystem therefore altering the structure and function of reefs (Dulvy et al. 2004, Hughes et al. 2007). Another prominent indirect anthropogenic impact is the change in global climate.

Global climate change is caused by rising atmospheric CO_2 concentrations. CO_2 levels have increased from 280 ppm in the pre-industrial era to present day levels of 403 ppm (Dlugokencky & Tans 2016). CO_2 levels are expected to reach between ~650 and ~1370 ppm by 2100 under the representative concentration pathways (RCPs) 4.5 and 8.5, respectively (Moss et al. 2008, Detlef et al. 2011). Ocean temperatures in most tropical regions have increased by nearly 1°C in the past 100 years (Ateweberhan et al. 2013). If greenhouse gas emissions are not reduced, temperatures are projected to increase by 3.7°C to 4.8°C at the end of the century (IPCC Fifth Assessment Report, 2014). While tropical reef systems have existed since the Cambrian period (542 million years ago), elevations in ocean temperature and declines in pH caused by anthropogenic climate change are projected to occur at a significantly faster rate than any time in the past 420,000 years (Buddemeier et al. 2004, Hoegh-Guldberg et al. 2007). This is projected to lead to the degradation of reef habitat and suppression of reef growth with unknown consequences for the future (Hughes 1994, Hughes et al. 2003, Hoegh-Guldberg et al. 2007).

A consequence of climate change is coral bleaching where elevated seawater temperatures result in the breakdown of the symbiotic relationship between corals and *Symbiodinium.* In this process, *Symbiodinium* are expelled from the coral tissue and the coral loses its pigmentation (Hoegh-Guldberg & Smith 1989). *Symbiodinium* provide corals with up to 90% of the energy needed for growth, reproduction and calcification (Falkowski et al. 1984). If *Symbiodinium* are lost, corals suffer from depletion of energy reserves in their tissues, which leads to reduced fecundity, reduced skeletal growth and increased susceptibility to disease (LaJeunesse 2002, Fabricius et al. 2004, Baker et al. 2008). If the bleaching is very severe and/or prolonged, corals may die (Glynn 1996). Over the last three decades, almost all tropical/subtropical reefs have been affected by bleaching (Baker et al. 2008). In 1998 a mass-bleaching event occurred due to a severe El Niño Southern Oscillation (ENSO) and warming of the tropic regions in the Northern Hemisphere (Berkelmans & Oliver 2004, Garpe et al. 2006). Reef systems in the Seychelles Islands experienced up to 75% coral mortality, Western Australia lost up to

90% of coral cover, and the Maldives up to 99% (Goreau et al. 2000). In recent years there has been an increase in regional bleaching events that occur every year or two in many parts of the world including in the Atlantic/Caribbean, Indian and Pacific Oceans (Joshi et al. 2015, Kuffner et al. 2015, Ainsworth et al. 2016). As a result, scleractinian coral cover has been declining (colonies are dying or experiencing partial mortality; average colony dimensions is shifting towards smaller sizes) and species composition is changing, with negative impacts on entire coral reef communities (Ruzicka et al. 2013, Pisapia et al. 2015).

1.2 Effects of thermal stress on early-life stages

Hundreds of studies have concluded that thermal stress events (i.e. bleaching) has a negative impact on adult coral colonies (Cook et al. 1990, Glynn & D'Croz 1990, Glynn 1996, Berkelmans et al. 2004, Moore et al. 2012, Ainsworth et al. 2016) . Recently, experimental studies are starting to include early life stages because these are recognized as being sensitive to environmental change (Byrne 2011). The early life stages of a coral are extremely important for the persistence of populations and recovery from disturbances. Larval availability, successful settlement and recruitment are the most important processes of maintenance and recovery in reef ecosystems (Ritson-Williams et al. 2009). For example, Scott Reef in Northwestern Australia recovered after a severe bleaching event due to high rates of growth and survival of remnant colonies, followed by a rapid increase in juvenile recruitment as colonies matured, i.e. a significant proportion of larvae produced by the remnant colonies successfully recruited back to the reef (Gilmour et al. 2013). The reproduction of corals is influenced by several factors such as lunar and diel cycles, ocean temperatures and chemicals (Willis et al. 1985, Chornesky & Peters 1987). Sexual reproduction includes several steps: gamete production and fertilization, larval development and dispersal, and metamorphosis/settlement (Fadlallah 1983, Ritson-Williams et al. 2009, Harrison 2011). Scleractinian corals have one of two sexual reproductive modes (Van Moorsel 1983, Ayre & Resing 1986, Jackson 1986, Baird et al. 2009). Brooding, where sperm is released into the water column and is taken in by conspecifics for internal fertilization

(Fadlallah & Pearse 1982, Szmant 1986), and broadcast spawning, when both the egg and sperm are released into the environment and fertilization occurs in the water column (Fadlallah 1983, Harrison et al. 1984, Szmant 1986).

Thermal stress can affect the reproduction and larval development of marine species (Ianora et al. 1992, Negri et al. 2007, Nozawa & Harrison 2007, Polato et al. 2010) which can lead to decreased larval dispersal and recruitment success (Omori et al. 2001, O'Connor et al. 2007, Edmunds et al. 2011) . Exposure to thermal stress in one life stage can affect the following life stages or future generations. Exposure of adults to a stress can negatively affects their offspring; this is termed negative parental effects (Mousseau & Dingle 1991, Fox et al. 1995). For instance, Green & McCormick (2005) reared eggs and larvae of the clownfish species *Amphiprion melanopus* at ambient and heated temperature treatments. While rearing temperature did not significantly affect the eggs or larvae, the conditions that parents were raised in showed differing results. Larvae whose parents were raised in the heated treatments had negative effects on metamorphosis and declined growth rates when compared to larvae whose parents were not exposed to the same temperature treatments (Green and McCormick 2005). Exposure to a thermal stress in one life stage that negatively affects the next life stage within a generation is termed latent effects (Pechenik 2006). Examples of latent effects include delayed metamorphosis, salinity stress and nutritional stress. For example, competent larvae of the common slipper shell deprived of food for two to five days metamorphosed earlier, but displayed slower juvenile growth even in the presence of excess food (Pechenik et al. 1996).

1.3 How corals can cope with thermal stress

Thermal stress can affect all life stages of marine organisms (Harley et al. 2006, Putnam et al. 2010, Byrne 2011, Byrne & Przeslawski 2013). Many tropical organisms live near or above temperatures that are optimal for performance, making tropical species more vulnerable to climate change (Tewksbury et al. 2008). Organisms can use an array of mechanisms to cope with elevated temperatures. These include associating with

thermally-tolerant symbionts, changes in the distribution range and/or behavior, adaptation and acclimation (Douglas 2003, Hughes et al. 2003).

For corals, associating with thermally-tolerant *Symbiodinium* species may be beneficial way to cope with climate change (Jones 2008, Silverstein et al. 2014). Corals can either switch symbionts, which is the acquisition of new symbionts from the environment, or shuffle the relative composition of its symbionts, making thermally-tolerant symbionts become more dominant over others (Baker et al. 2003). Following two consecutive bleaching events, two pocilloporid coral species showed evidence of acquiring thermally-resistant clade D *Symbiodinium* from the environment indicating that the switching may have been a result of the thermal bleaching events (Boulotte et al. 2016). Most broadcast spawners and some brooding corals do not provide *Symbiodinium* to their offspring, therefore corals need to acquire symbionts in each generation from the water column. The uptake of *Symbiodinium* in each generation provides corals with a means to shuffle *Symbiodinium* types (Cumbo et al. 2013). During the initial establishment of symbiosis corals are promiscuous, associating with multiple types of symbionts not generally found in the adults (Cumbo et al. 2013). Acclimation to new environmental conditions may be possible if, after acquiring multiple *Symbiodinium* species during the larval or juvenile stage, corals select the most appropriate species for the environment they face in later stages of development (Cumbo et al. 2013). This possibility of acquiring multiple *Symbiodinium* types in the early life stages is likely an adaptive trait. However, while the initial association with multiple *Symbiodinium* species is flexible, adult corals are generally dominated by one symbiont type, and their growth rates is partially dependent on the symbiont type selected earlier in development (Baker 2003).

Another way corals may cope with climate change is through migration. Though adult scleractinian corals are sessile, coral larvae are planktonic. Larvae will obligatorily disperse until they become competent to settle and metamorphose (Fadlallah 1983, Babcock et al. 1986). After acquiring competency, larvae still need to find a suitable place to settle, which may extend their dispersal period. Coral larvae are lecithotrophic,

relying on lipids derived from their mother as their main energy reserve when in the water column (Kemph & Hadfield 1985, Jaeckle & Manahan 1989). Thus, the duration and timing of the larval dispersal is highly dependent on the amount of maternal reserves, currents and proximity of reefs (i.e. availability of suitable substrate) (Hellberg 1996, Miller & Mundy 2003). The planktonic nature of their larvae allows corals to spread out into different geographic areas covering a range of temperatures. Elevation of seawater temperatures may allow coral larvae that disperse to higher latitudes to survive and thus expand or shift coral distribution to previously unpopulated sub-tropical areas (Jokiel 1984, Fisk & Harriott 1990, Chadwick-Furman & Loya 1992, van Oppen et al. 2008).

Over time, populations can adapt to new environmental conditions as gene mutations accumulate and better-adapted individuals are positively selected (Brown 1997). While environmental changes may exceed the adaptive capacity for species with low intrinsic growth rates and long generation times, such as corals, species may still have a chance to persist through processes of acclimatization (Munday et al. 2013). Acclimation consists in a change in the physiological response(s) of an organism to an experimentally altered single environmental variable, while acclimatization is the change of physiological response(s) to environmental variables in the field (Wilson & Franklin 2002). In addition to physiological responses, organisms can modify behavioral and morphological characteristics in order to function normally regardless of the environmental changes experienced (Munday et al. 2013). For example, the bivalve *Mytilus galloprovincialis* lives in temperatures that are close to their acclimation limits where a small degree of warming can trigger stress responses in the organism at whole and molecular levels such as shifting from aerobic to anaerobic metabolism or valve closure (Anestis et al. 2007). The degree to which corals are able to undergo genetic adaptation or physiological acclimatization in response to thermal changes is partially unknown yet studies have described the possibility for each (Howells et al. 2013, Palumbi et al. 2014, Putnam & Gates 2015).

Corals that live in areas with high frequency of bleaching events have showed signs of adaptation over time (van Woesik et al. 2011). For example, two reefs in Palau,

Micronesia had cooler temperatures and were partially shaded compared to a lagoon reef that had chronically higher temperatures. Despite the higher temperatures and frequent bleaching events, the lagoon reef did not experience such high coral mortality as the colder reefs during a bleaching event that occurred in 1998. Most likely the coral and symbionts in the lagoon reef had adapted to elevated temperatures, and/or the corals associated with a higher concentration of thermally tolerant symbionts (Fabricius et al. 2004). Corals can also acclimate to warmer microclimate conditions and have developed resistance to bleaching without changing symbionts. For example, corals were reciprocally transplanted between reef sites that had distinct temperature regimes. In a little over two years, their physiological and gene expression profiles revealed that the corals had acclimatized, having the same heat tolerance that the is only expected to be attained from natural selection over multiple generations (Palumbi et al. 2014).

1.4 Acclimation in corals

There are three types of acclimation: reversible, developmental and transgenerational (Donelson et al. 2011a, Miller et al. 2012). Reversible acclimation occurs as short-term regulated responses to diel or seasonal changes in temperature (Munday et al. 2014). For example, the desert night lizard's body temperature has a profound influence on their sprinting speed. Their typical maximum speed occurs at 33-34°C but when exposed to extreme lower temperature that occurs in the desert at night (ca. 20°C), the lizard runs faster than when at 30°C (Kauffman & Bennett 1989). Developmental acclimation relates to responses (changes in phenotype) to different environmental conditions during early ontogeny (embryonic and larval development) that are maintained through the rest of the organism's life (Munday et al. 2013). Organisms with a dispersive larval stage, such as reef fish and coral, will likely utilize developmental acclimation in order to acclimate to changes in environmental conditions following long distance dispersal (Form & Riebesell 2011). For example, adult zebrafish reared at optimal temperature, but whose embryos were incubated at warmest temperature within their range for normal development displayed improved swimming performance at higher temperatures (Scott and Johnston 2012). Parents can further increase the fitness of

offspring by providing them with defensive agents, symbionts, pathogens, toxins, hormones and enzymes. Manipulating the expression of the offspring genome through the inclusion of compounds in the eggs that up or down regulate certain genes to develop a locally-fit phenotype can also occur (Rossiter 1996). Transgenerational acclimation depends on the environmental variables or stress that the parents experience. For example, elevated temperatures and CO_2 increase the metabolic rate and decreased weight, length, and survival of juvenile anemonefish *Amphiprion melanopus*. However, these effects were absent or reversed in juveniles whose parents were conditioned to elevated-CO_2 and temperature conditions (Miller et al. 2012).

2. OBJECTIVES

The aim of my study was to explore the within-generation capacity of corals to acclimate to ocean warming through developmental acclimation. Specifically:

1) Determine the effect of temperature on larval survival and size at settlement;
2) Quantitatively determine the capacity for developmental acclimation in corals;
3) Assess latent effects of exposure to warmer conditions during larval development on juvenile survival and growth.

Note: To determine if the *Symbiodinium* composition in the juveniles is dependent on the temperature experienced during the larval and/or juvenile stages and if it ultimately affects their growth, the symbiont composition within samples of adults and juveniles is currently being analyzed at the University of Buffalo. Due to time constraints described above, these results will not be part of my thesis.

3. METHODOLOGY

3.1 Study species

Montastraea cavernosa was chosen as the study species for this project due to its abundance, spawning habits, shallow depth range (10-30 meters) and its importance in the south Florida reef tract system. Often referred to as the great star coral, *M. cavernosa* is a common reef-builder found in the Atlantic and Caribbean regions and can tolerate turbid or silty environments (Kelmanson & Matz 2003, Serrano et al. 2014). Individuals grow in fairly small colonies and form structures that are usually dome-shaped, boulders or grow in flat plates (Veron 2000) (Fig. 1). The color of *M. cavernosa* can vary, ranging from green and brown to orange and red (Acosta & Zea 1997). The species is a gonochoric broadcast spawner, with spawning usually taking place a few days after the full moon in July-September (Szmant 1991). Being a spawner allows for easier assessment of developmental acclimation because embryogenesis and larval development occur in the water column (Thornhill et al. 2006), and thus effects of stress during this life stage cannot be confused with parental effects.

Fig. 1: *Montastraea cavernosa* colony (Photo: Peter Grasso)

3.2 Coral collection

Thirteen colonies of *M. cavernosa* were collected August 26th, 2015, three days before the full moon (Szmant 1991, Acosta & Zea 1997), via scuba from sites located offshore Broward County, Florida, U.S.A. (Fig. 2). The colonies had ca. 30 cm in diameter and were removed from the reef using hammers, chisels, and prybars. After being detached and brought to the boat using dish racks, the colonies were immediately wrapped in bubble wrap to avoid desiccation and placed in coolers to maintain temperature. Sediment was also collected at each site to be used for future symbiont exposure (see sediment collection section). Corals were then transported to Nova Southeastern University's Guy Harvey Oceanographic Center (NSU GHOC) and maintained in a 1500L outdoor recirculating tank with controlled temperature (using a heater and a chiller). Water was maintained at 29°C, which is the ambient summer temperature in Broward County (Moyer et al. 2003). Natural light conditions were used in conjunction with shade cloths to mimic solar noon irradiance levels (215 µmol photons/m^2s) measured with a Li-Cor® Li-250A light meter in the field. All colonies maintained adequate health and were returned back to the original collection site on September 30th 2015. Collections were permitted by Broward County (DAN1410-037) and Florida Fish and Wildlife (SAL-15-1645-SCRP).

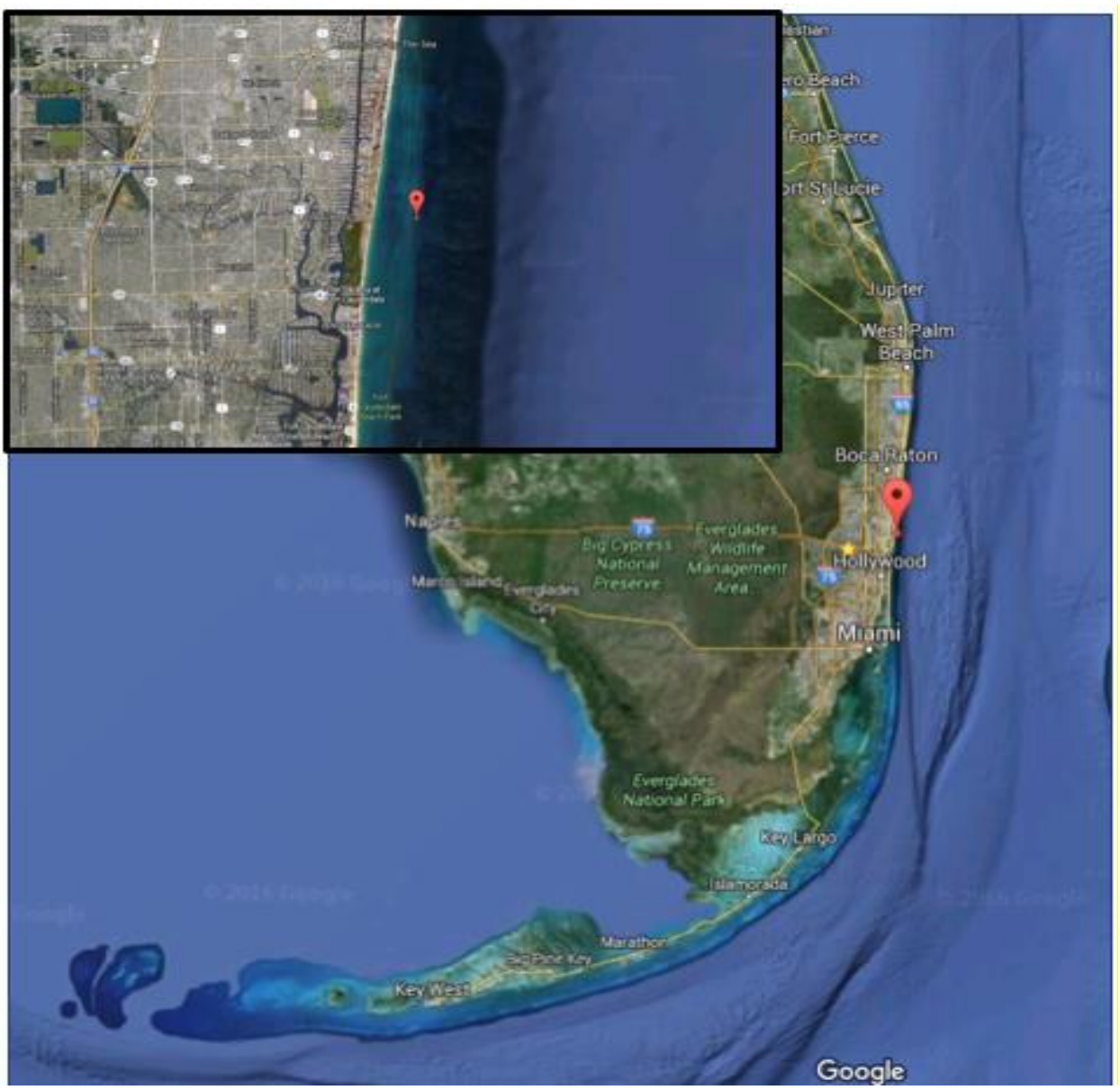

Fig. 2: Location of coral collection offshore Broward County, FL (inset) along SE Florida Reef Tract (26.153790 N, -80.089183 W), 2015

3.3 Sediment collection

Sediment was collected at the same sites the corals were collected to provide juveniles with a realistic diversity of *Symbiodinium*. The top oxygenated layer of sediment was collected, which was expected to be a source of symbionts (Cumbo et al.

2013). The oxygenated layer is determined by its coloration: grey and black indicate anoxic conditions. The sediment was collected in plastic containers with seawater and placed in the coolers the corals were transported in to maintain temperature. Sediment was maintained in the outdoor recirculating tank with oxygenated seawater and under the same temperature/light regimes as the adult coral colonies.

3.4 Gamete collection/fertilization

Starting at sunset each day after collection, colonies were placed in separate buckets with saltwater taken from their aquarium. Corals were checked for gametes every thirty minutes for spawning activity. If there were gametes, eggs were positively buoyant and gently collected from the top of the container. Sperm was collected using a baster. Careful consideration was taken in both instances to not collect excess water so that the gametes were not diluted. The collected gametes were then taken into the lab and combined, using a sperm concentration of 10^6 per mL. After one hour, eggs were placed under the microscope to assess fertilization, identified by egg cleavage. When more than 80% of embryos had undergone the first division, the sperm was flushed out.

3.5 Larval survival

To determine the effects of temperature on larval survival, thirty minutes after fertilization, embryos were placed in 200mL glass jars (50 embryos per jar) with filtered seawater and reared at: 29°C, Broward County ambient seawater temperatures in summer and 31°C, projected temperature under climate change for year 2050 under scenario RCP 8.5 (IPCC Fifth Assessment Report, 2014). This experiment was conducted with eight replicates (jars) per temperature. Larvae were counted (and water was exchanged) daily until all larvae died (79 days).

3.6 Larval culture

To assess the capacity for developmental acclimation, an orthogonal design was used (Fig. 3). Specifically, thirty minutes post-fertilization, embryos were separated into two temperature treatments: 29°C and 31°C. Larvae were reared in 1L plastic bowls with filtered seawater at a density of less than 1 larvae mL^{-1} with at least eight bowls per temperature. Bowls were placed in water baths equipped with heaters and small pumps that allowed water circulation to equalize temperature throughout. Water changes took place daily until larvae reached competency.

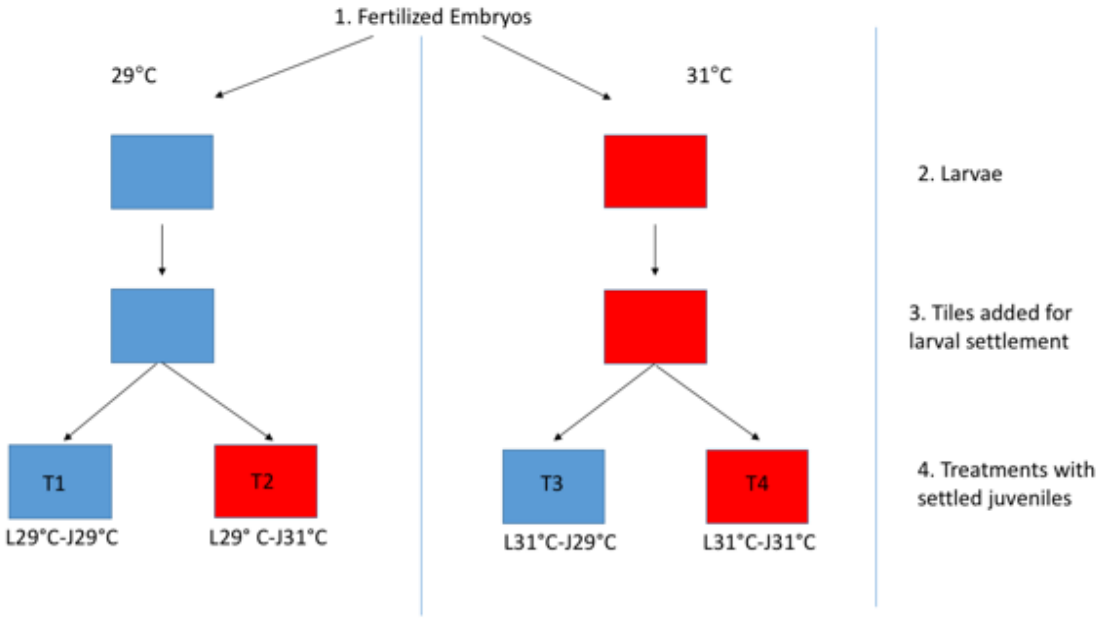

Fig. 3: Experimental design for larval and juvenile cultures

3.7 Larval settlement

Larval settlement was determined by using ceramic settlement tiles (2 x 2 x 0.5 cm) that had been conditioned for two months in reefs located off the coast of Broward County, FL in coral nurseries maintained by Dr. Gilliam, National Coral Reef Institute at NSU. Motile larvae were moved to 200mL glass jars (20 larvae per jar) containing a pre-conditioned settlement tile to induce settlement and metamorphosis. The tiles were

removed and replaced daily (Fig. 3). The removed tiles were examined in a water bath using a stereo-dissecting microscope and the number of larvae completing metamorphosis and location on the tile were recorded. The coral polyps were photographed using a camera (Olympus LC20) mounted in the stereoscope to determine surface area and posterior ease the tracking of survival and growth. The settlement experiments were conducted until the majority of larvae have settled in each jar. Since a different amount of larvae settled every day, the settlement date was recorded for each individual and following survival and growth measurements were done weekly from this date (see below).

3.8 Juvenile culture

Newly settled juveniles that were exposed to either 29°C or 31° temperature during the larval stage were reared at either ambient (29°C) or elevated temperature (31°C) for a total of four treatments (Fig.3, Table 1). Juvenile that were experiencing a change in temperature (i.e. treatments 2 and 3, Table 1) were slowly acclimated to the new temperature over a 48-hour period (0.5°C/12hrs).

Table 1: Treatment name and temperature combinations for the larvae (L) and juvenile (J) *M. cavernosa* survival and growth experiments

Treatment Name	Temperature Combinations (Larval-Juvenile)
Treatment 1 (T1)	L29°C-J29°C
Treatment 2 (T2)	L29°C-J31°C
Treatment 3 (T3)	L31°C-J29°C
Treatment 4 (T4)	L31°C-J31°C

Juveniles were reared in tanks with a 12:12 hour light:dark photoperiod to mimic natural light conditions, sunrise being at 0700 and sunset at 1900, using controllable LED lights. Submersible aquarium 300 watt heaters (Programmable EHEIM® Jager) were

placed in each tank to maintain temperature (29°C and 31°C ±0.1ºC) . Submersible pumps (SunSun® JP-032) were used create a water flow and thus provide oxygen throughout the tank (Fig. 4). Water used in the tanks was previously filtered by mechanical and biological filtration, a protein-skimmer and UV sterilizer. Nitrate, nitrite, ammonia, and phosphate were monitored every few days. Fifty percent water changes took place three times per week and one 100% water change took place once per week. Sediment containing symbionts was maintained in the outdoor flow-through tanks that the adult colonies of *M. cavernosa* were placed in. Sediment was wet-sieved into buckets and washed through a 25µm filter to remove excess microbes and debris. This process was repeated about three to four times or until the drained water was clear. After the filter was cleaned, washes were done and the water collected was used to add to the water changes. During water changes, 8L of seawater containing *Symbiodinium* was added to each tank to provide exposure of juveniles to symbionts. Juvenile survival and growth was assessed each week under the dissecting scope and using CellSens® to measure the surface area of individual polyps. Juveniles were reared in these conditions for a period of eight weeks. After the end of the experiment, surviving juveniles were used for genetic analysis to identify the types of *Symbiodinium* present.

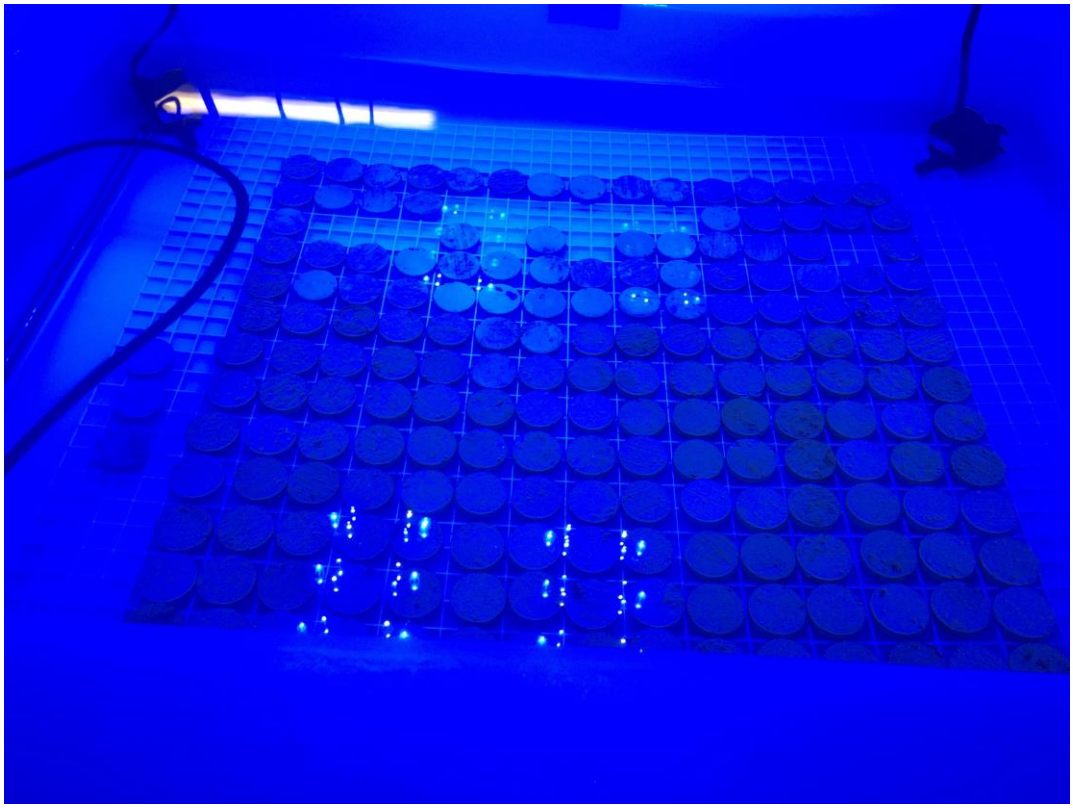

Fig. 4: Juvenile tank set-up with juveniles on ceramic tiles (Photo credit: Heather Schaneen)

3.9 Symbiodinium identification

To identify the clades of *Symbiodinium* acquired by the corals, the genetic samples of surviving juveniles were preserved following the termination of the survival and growth experiments using CHAOS buffer and magnetic beads. CHAOS was prepared using: 4M guanidine thiocyanate (100g), 0.5 N-Laurosil-sarcosine (1 g), 25uM Tris pH 8.0 (5 ml), 0.1m 2-mercapto ethanol (1.4 ml) and ultra pure water. Tris was made using Tris base (15.4 g), distilled water (100ml) and HCl (5.25 ml). In preparation for genetic analysis, the juvenile samples were placed in a CHAOS mixture (5/drops sample) and vortexed. All the liquid from the samples were placed in individual wells. Ten mL of magnetic beads were added to each well and then mixed with 50mL of isopropyl. A

magnetic plate with a lid was placed on the plate for five to ten minutes to have the magnetic beads move down in the wells. After, the wells were drained of excess liquid by turning the plate upside down. 200 mL of cold ETOH was then added with a multi-channel pipette and drained as a wash. This was repeated five times. After the final drain, samples were then allowed to dry for 45-60 minutes, and then 35mL of TE was added to each sample and placed on a shaker for 80-90 minutes. The magnetic plate was placed back on the samples for 10 minutes before 50µL of supernatant was pipetted out of the center of the wells and into new containers. These samples were preserved at -20°F and DNA was quantified using Nanodrop. Samples were packaged and sent off to Dr. Mary Alice Coffroth (University of Buffalo) for further analysis.

3.10 Data analysis

Larval survival at the two temperatures was compared using survival analysis, specifically, a Mantel-Haenszel (log-rank) test. The size (surface area) of the newly-settled juveniles was compared using a t-test (or equivalent Kruskal-Wallis test, if the assumptions were not met). Juvenile survival was compared between treatments using survival analysis, specifically, a Mantel-Haenszel (log-rank) test. If treatments were found to be significantly different, pairwise tests (Mantel-Haenszel) were done to determine if exposure to warmer conditions during the juvenile stage led to higher mortality (Treatments 1 vs. 2), if there were latent effects of exposure to warm conditions during the larval stage (Treatments 1 vs. 3), and if there was developmental acclimation (Treatments 2 vs. 4). Survival curves were plotted using a Kaplan-Meier estimator. Growth (polyp surface area) over eight weeks was compared between treatments by fitting an exponential model to the growth data. The initial size of the polyps (constant parameter of the exponential equation) was forced to equal the average of each two treatments which were reared under the same larval conditions. This allowed the comparison of the growth rate parameter (exponent in the exponential equation). All statistical analysis were performed using software R Studio®.

4. RESULTS

4.1 Larval survival and size at settlement

Larvae reared at warmer conditions displayed lower survival than larvae reared at ambient conditions (χ^2= 26.3, df=1, p= 2.88x10^{-7}, Fig. 5), and displayed a smaller size at settlement (χ^2= 14.4, df = 1, p= 0.000146, Fig. 6).

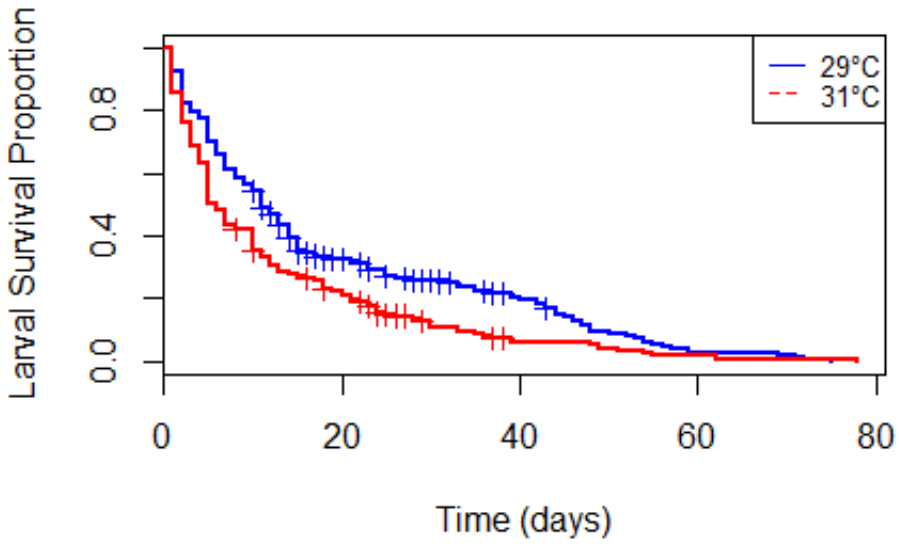

Figure 5: Kaplan-Meier Survival curves for larvae reared at 29 and 31°C

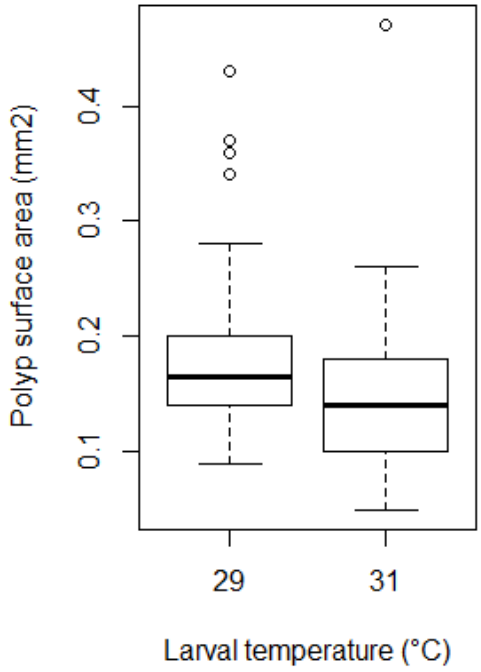

Figure 6: Size (surface area) at settlement when reared at 29 and 31°C during larval stage

4.2 Juvenile Survival

Juvenile survival significantly differ between treatments (χ^2= 8.5, df=3, p= 0.0369, Fig.7), specifically: 1) survival of juveniles in Treatment 1 (L29°C-J29°C) was greater than in Treatment 2 (L29°C-J31°C) (χ^2= 4, df=1, p= 0.0451, Fig. 7) which suggests that exposure to warmer temperatures during the juvenile stage led to increased mortality; 2) survival of juveniles in Treatment 1 (L29°C-J29°C) was greater than in Treatment 3 (L31°C-J29°C) (χ^2= 6.5, df=1 , p= 0.0111, Fig. 7) which suggests that exposure to warmer temperatures during the larval stage led to increased mortality during the juvenile stage (latent effects); and 3) survival of juveniles in Treatment 4 (L31°C-J31°C) was not significantly different than in Treatment 2 (L29°C-J31°C) (χ^2= 0.1, df=1, p= 0.704, Fig. 7), which suggests that exposure to warmer conditions during the larval stage does not confer higher resistance to warmer conditions on the following life stage

(i.e. no developmental acclimation).

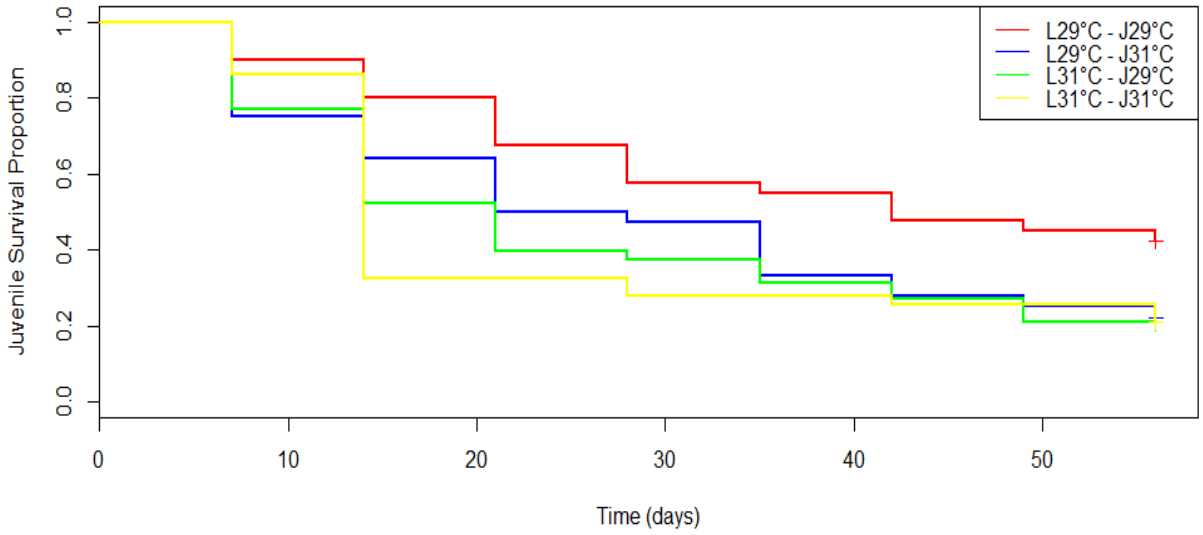

Figure 7: Kaplan-Meier survival curves of juveniles from Treatments 1 (L29°C-J29°C), 2 (L29°C-J31°C), 3 (L31°C-J29°C), and 4 (L31°C-J31°C).

4.3 Juvenile Growth

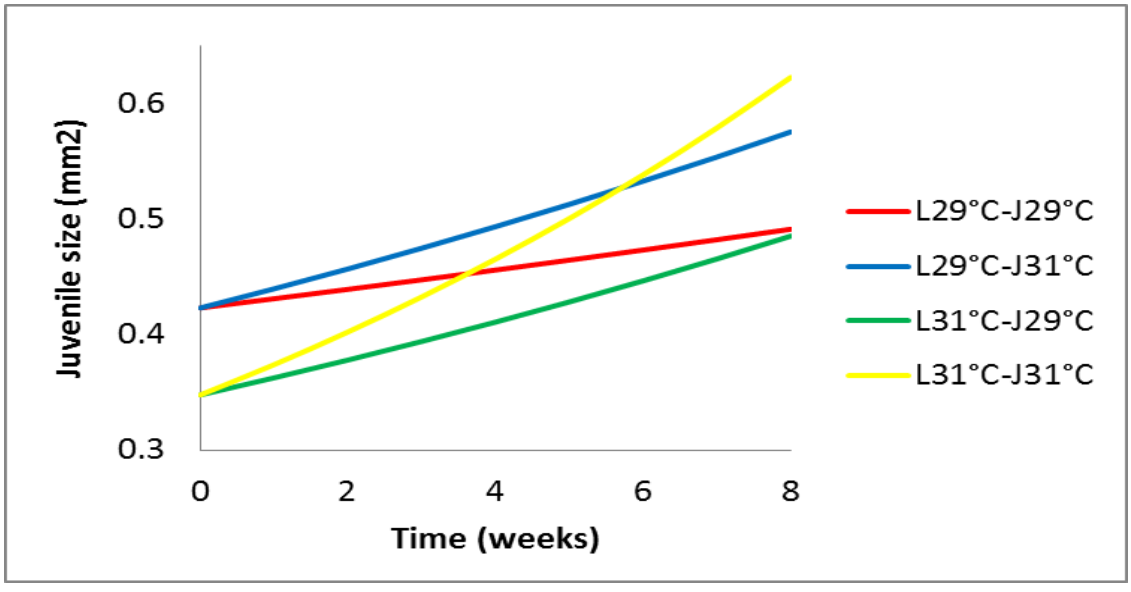

Figure 8: Exponential growth models for the juveniles in Treatments 1 (L29°C-J29°C), 2 (L29°C-J31°C), 3 (L31°C-J29°C), and 4 (L31°C-J31°C).

Juveniles reared at warmer conditions displayed higher growth rates than juveniles reared at ambient conditions: Treatment 2 (L29°C-J31°C) had a greater growth rate (0.0385mm^2/week) than Treatment 1 (L29°C-J29°C, 0.0187mm^2/week), and Treatment 4 (L31°C-J31°C) had a greater growth rate (0.0729mm^2/week) than Treatment 3 (L31°C-J29°C, 0.0417mm^2/week) (Fig. 8). Exposure to warmer conditions during the larval stage led to faster growth on the following life stage. Specifically, the growth rate of juveniles on Treatment 4 (L31°C-J31°C, 0.0729mm^2/week) was greater than on Treatment 2 (L29°C-J31°C, 0.0385mm^2/week), and growth rate of juveniles on Treatment 3 (L31°C-J29°C, 0.0417mm^2/week) was greater than on Treatment 1 (L29°C-J29°C, 0.0187mm^2/week) (Fig. 8), These results indicate that there was no latent effects for juvenile growth of exposure to warmer temperatures during the larval stage and developmental acclimation may have occurred (but see discussion).

5. DISCUSSION

Elevation in temperature increased larval mortality (Fig. 5). In addition, individuals that were exposed to the elevated temperature during larval development displayed a smaller polyp size at the time of settlement (Fig 6), and higher mortality during the juvenile stage (Fig. 7). These results indicate that exposure to thermal stress during larval development is deleterious and has latent effects. Juveniles grew faster when exposed to warmer conditions (Fig. 8), but also displayed higher mortality (Fig. 7), therefore no developmental acclimation was found in regards to their survival. The higher growth rates displayed by juveniles exposed to higher temperatures during the larval stage could indicate developmental acclimation in regards to growth. However, the higher growth rates under warmer conditions could have also been caused by a positive selection (during the larval or juvenile stage) of the most thermally-resistant juveniles (if

these were the greatest size individuals), which ultimately may have positively skewed the growth rates.

Higher temperatures had a negative effect on the survival of larvae. Overall mortality in the 31°C treatment was higher than in the 29°C treatment (Fig 5). This difference was established within on the first few days. Increased larval mortality may occur at elevated temperatures because enzyme activity, which accelerates biochemical processes and metabolic rates, also increases (Jobling 2002, Clarke & Fraser 2004) and consequently so does larval development (Woolsey et al. 2015, Figueiredo et al. 2014). A faster rate of cell division ultimately increases the likelihood of embryos/larvae being abnormal and thus experiencing higher mortality rates (Albright & Mason 2013, Arnberg et al. 2013). When testing the effect of increased temperatures on the larval development of several different scleractinian coral species, Negri et al. (2007) found that *Acropora millepora* embryos displayed abnormalities when exposed to 32°C. In my study, mortality rates at both temperatures become more similar after one week. This is likely because the planula stage was reached and thus no major cell division were taking place. This interpretation agrees with the findings of Randall & Szmant (2009) which studied the effect 2°C increase on the larvae of the brooding coral *Favia fragum* (note that brooding species release already formed planula) and did not find a significantly different larval mortality. Alternatively, the higher temperature in the first week may have selected the individuals that can cope with higher temperatures (killing the less thermally-tolerant) and thus, after that period, the survivors died at a similar rate as the larvae reared at 29°C.

Larvae that were raised in the heated treatment displayed smaller polyp surface area at time of settlement (Fig. 6). Broadcast spawners such as *M. cavernosa* have lecithotrophic larvae (Byrne et al. 2003, Kerr et al. 2011) and thus rely on maternally-derived lipids energy reserves (Vance 1973). Elevated temperature increases larval metabolism therefore depleting their energy reserve more quickly (O'Connor et al. 2007). Newly-settled juveniles of *M. cavernosa* likely had smaller polyp sizes at settlement due to the elevated temperature increasing their metabolism (Clarke & Fraser 2004) and using up a significant portion of their lipid contents, which accounts for the majority of a

larva's biomass (Figueiredo et al. 2012) The smaller size of individuals at time of settlement yields possible implications in terms of growth of that individual in the future. For instance, individuals retaining a smaller polyp size throughout life could experience decreased fecundity and egg production (Chornesky & Peters 1987, Sakai 1998).

Temperature significantly affected juvenile survival with individuals exposed to warmer temperatures during the juvenile stage displayed higher mortality (Fig. 7). As in the larvae, this may have been due to the acceleration of metabolism under warmer conditions (Clarke & Fraser 2004), and thus a faster consumption of the energy reserves. In this study, juveniles of *M. cavernosa* were not fed, therefore the only source of energy they had access to was their symbionts. The juveniles did acquire *Symbiodinium* (visible through pigmentation) however, symbiont density may have been insufficient to compensate for the juveniles energy consumption at higher temperatures. It is unknown if feeding could have minimized or even eliminated the differential survival between the current and elevated temperature treatments, as it has been shown in a previous study with adult corals (Edmunds 2011). Future studies should assess if feeding of coral juveniles during experiments could yield different results.

Exposure to elevated temperatures during the larval stage did not show higher resistance to warmer conditions in the juvenile stage, indicating that no developmental acclimation occurred. In fact, the exposure to warmer temperatures during the larval stage had latent effects, specifically, higher mortality during the juvenile stage. Latent effects originate in the embryonic or larval stage and may have only become visible in the juvenile stage (Pechenik, 2006). Exposure to projected ocean warming temperatures have resulted in latent effects (such as size, frequency of malformations and survival) of many marine organisms (i.e. reef fish and squid; Donelson et al. 2011b, Pankhurst & Munday 2011, Rosa et al. 2012), including corals. For example, larvae of the broadcast spawning species *Acropora solitaryensis* reared at higher temperatures had a lower post-settlement survival (Nozawa & Harrison 2007). In the brooder *Porites astreoides*, exposure to thermal stress during the larval stage also led to increased juvenile mortality (Ross et al. 2013). Since corals are a long-lived species and have slow growth rates, it is difficult to

conduct studies to assess if elevated temperatures affect overall growth and survival, but models have predicted that decreased survival and size will be likely occur with increases temperature (Cantin et al. 2010). Long-term studies that monitor survival and growth of the whole life cycle of a coral (larval, juvenile, adult) are needed to assess negative and positive effects of stress across life stages and generations (Munday et al. 2013).

Juveniles that were reared at warmer temperatures had higher growth rates than those that were raised at ambient conditions (Fig. 8). Additionally, exposure to warmer conditions during the larval stage led to faster growth rates in the juvenile stage. Individually, these results seem to indicate that there were no latent effects for juvenile growth and that developmental acclimation occurred. The adults of this species have been previously found to tolerate high temperatures without a depression in growth (Manzello et al. 2015), thus it is plausible that growth rates may not be negatively affected by temperature. However, when these results are considered along with juvenile survival (which led to opposite results, i.e. latent effects and no developmental acclimation), they can indicate otherwise. Rather than developmental acclimation, potentially positive selection of the most fit individuals under high temperatures has occurred. Specifically, the higher growth rates may have been artificially produced by higher mortality rates within the smaller sized juveniles in the first few weeks. This would skew the overall juvenile size to greater sizes later in development, thus producing a higher growth rate for the full eight-week period. Furthermore, the smallest juveniles, among those reared under warmer conditions during the larval stage and then kept at ambient conditions during the juveniles stage, could have died at a higher rate during the juvenile stage (due to latent effects, exhaustion of energy reserves), which then inflated the overall growth rate. Alternatively, these results may be explained by differences in symbiont compositions among juveniles in the different temperature treatments. The adult broodstock and juveniles reared in all treatments were sampled and are currently being analyzed to genetically identify their *Symbiodinium*.

It is still not know whether corals will be able to persist at higher temperatures (Munday et al. 2013). New models predict that coral adaptation over a 40-year time

period could drastically alter predictions for the demise of coral reefs (Logan et al. 2014). Corals' ability to undergo physiological acclimatization in response to increased thermal changes remains unclear (Howells et al. 2013). Here we found no developmental acclimation, however transgenerational studies have shown acclimation of corals to thermal stress across generations (Putnam & Gates 2015) and some adult corals can acquire resistance to temperature relatively fast (Palumbi et al. 2014). Additional studies are needed to produce more evidence of physiological acclimatization, particularly across multiple life stages and whether the feeding or non-feeding of larvae/juveniles has an effect on coral survival and growth (Ross et al. 2013). Unfortunately, these experiments are somewhat difficult due to the slow-growing, and long-life of corals. With increasing technology, more research into the areas of adaptation and acclimation will help producing more accurate predictions of future coral abundance, diversity and community composition.

Regardless if there is developmental acclimation or not, my study shows that ca. 30% of larvae can survive projected temperature under climate change for year 2050 under scenario RCP 8.5 (IPCC Fifth Assessment Report, 2014) for two weeks. In this period of time, larvae have acquired competency and can settle to start creating reef structure. Furthermore, of the 30% of individuals that survive warmer conditions through the larval stage, 30% survived as juveniles for eight weeks in unfed conditions, indicating that at least 9% of the original population can survive 2050 temperatures. However, latent effects may have negative consequences in later stages of development. It is also possible that different species, or even different populations of the same species, may have differential ability to cope and adapt to higher temperatures (Hoey et al. 2016). For example, some coral populations such as those in the Arabian and Persian Gulf and Northern Red Sea can withstand temperatures up to 34°C, and thus have a much higher thermal tolerance than the great majority of corals populations elsewhere (Purkis et al. 2011, Riegl et al. 2011, Descombes et al. 2015).

The negative effects of global climate change and associated ocean warming cannot be successfully managed as a whole, but managers may possibly lessen the effects

regionally or locally (Berkelmans & van Oppen 2006, Dawson et al. 2011, Abelson et al. 2016). Some genotypes used in restoration methods often suffer mortality during bleaching events, showing that these are likely less thermally-resistant. The cross (through sexual reproduction) of thermally-resistant genotypes with less thermally-resistant genotypes may confer resulting offspring with higher thermal resistance without losing genetic variability. The offspring could then be reared under warmer conditions in the laboratory to select the most thermally-tolerant to be outplanted in areas which generally experience warmer temperatures. If successful, the utilization of these techniques may considerably increase the resistance of corals to thermal bleaching, at least in a local scale. However, more research needs to be conducted to determine whether the increased thermal tolerance of transplanted corals (Baker et al. 2008, Coles & Riegl 2013), could be undermined by other local anthropogenic impacts, such as pollution and sedimentation.

This study provides an assessment of how an important reef-building coral, *M. cavernosa*, may withstand future ocean temperatures. Most past and current studies have focused on evaluating the negative effects of climate change and developing models to predict future damage. A shift of focus to mechanisms that may aid in thermal tolerance may however be needed to complement existing information and inform managers on best procedures to sustain coral persistence.

ACKNOWLEDGEMENTS

My Committee members: Dr. Joana Figueiredo, Dr. Nicole Fogarty, and Dr. Vivian Cumbo for the ability to work with such inspiring and talented individuals and for their guidance throughout every aspect of this project

NSU Larval Ecology Lab members: A Kuba, F. Fourney, P. Grasso, A Nease, M. Knowles, N. Kornder, H. DeMarchis, A. Galarno and D. Lawson for their substantial help and time in assisting in everything from collecting corals to providing countless hours of thoughtful edits and suggestions

Family & Friends: Most notably A. Patranella, J. Caderas, and R. Zimmerman for time and contributions regarding this project and providing encouragement and friendship when it was needed most

My parents and family for their undoubted love, support and encouragement to pursue my love of the ocean

A.J. Macaluso and family for their constant love and praise and for being the best second-family there is

Keys Marine Lab: for the gracious use of their facilities and boat fleet and loaning out Captain Bill for all diving trips

This work was possible through funding from the NSU Presidential Faculty Research & Development Grant 2014 (#335341) & Marine Industries Scholarship.

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